Cerebral Cortex

Interplay between grip and vision in the monkey medial parietal lobe

Rossella Breveglieri, Marina De Vitis, Annalisa Bosco, Claudio Galletti, Patrizia Fattori

Department of Pharmacy and Biotechnology, University of Bologna, Piazza di Porta San Donato, 2, 40126 Bologna (Italy).

Running title: Grip and vision in V6A

Contact

Correspondence should be addressed to Prof. Patrizia Fattori, Dept. of Pharmacy and Biotechnology, University of Bologna, Piazza di Porta S. Donato, 2, 40126 Bologna, Italy. E-mail: patrizia.fattori@unibo.it; fax 00390512091737.

Keywords: area V6A; dorsal visual stream; hand-object interaction; superior parietal lobule; visual feedback

Abstract

We aimed at understanding the relative contribution of visual information and hand shaping to the neuronal activity of medial posterior parietal area V6A, a newly added area in the monkey cortical grasping circuit. Two *Macaca fascicularis* performed a Reach-to-Grasp task in the dark and in the light, grasping objects of different shapes. We found that V6A contains Visual cells, activated only during grasping in the light; Motor neurons, equally activated during grasping in the dark and in the light; Visuomotor cells, differently activated while grasping in the dark and in the light. Visual, Motor, and Visuomotor neurons were moderately or highly selective during grasping, whereas they reduced their selectivity during object observation without performing grasping. The use of the same experimental design employed in the dorsolateral grasping area AIP by other authors allowed us to compare the grasp-related properties of V6A and AIP. From these data and from the literature a frame emerges with many similarities between medial grasping area V6A and lateral grasping area AIP: both areas update and control prehension, with V6A less sensitive than AIP to fine visual details of the objects to be grasped, but more involved in coordinating reaching and grasping.

Introduction

Information about the physical characteristics of objects to be grasped (such as size, shape and orientation) and their spatial location is fundamental for the correct execution of a grasping movement. The ability to grasp objects relies on a network of areas in the parietal and frontal cortex (Jeannerod et al., 1995; Rizzolatti, 1997; Janssen and Scherberger, 2015; Fattori et al., 2017). Among areas involved in the grasping circuit, area V6A has been recently added; this area is located in the posterior parietal cortex (PPC), in the caudalmost part of the superior parietal lobule. V6A belongs to the dorsomedial visual stream (Galletti et al., 2003; Rizzolatti and Matelli, 2003), but is directly connected with the dorsolateral grasping parietal area (anterior intraparietal area, AIP) (Borra et al., 2008; Gamberini et al., 2009). Thanks to the seminal works by Sakata and collaborators (Taira et al., 1990; Sakata et al., 1995; Murata et al., 1996, 2000), who tested AIP neurons when grasping of different objects occurred in the light and in the dark, area AIP was proved to be involved in grasping actions. Moreover, it was shown that some AIP neurons received both visual and grip information ('Visual and Motor' neurons), some others received only visual input ('Visual dominant' neurons) and others only motor-related information ('Motor dominant' neurons) (Taira et al., 1990; Sakata et al., 1995; Murata et al., 2000). More recent works shed new light on other grasp-related properties of AIP, demonstrating that its neurons are modulated by the context of the grasping action (Baumann et al., 2009) and by directional signals of arm movements (Lehmann and Scherberger, 2013) and that signals from AIP can be used to decode grasping actions (Schaffelhofer et al., 2015; Schaffelhofer and Scherberger, 2016). Even more recently, it was demonstrated that AIP cells respond to the vision of one's own hand in action (Maeda et al., 2015) and that they are specialized in shape processing and processing of object features important for grasping (Gardner et al., 2007; Chen et al., 2009; Schaffelhofer and Scherberger, 2016).

Thanks to the functional properties of its neurons (Fattori et al., 2017), and to its connections with area AIP and premotor area F2 (Matelli et al., 1998; Shipp et al., 1998; Borra et al., 2008;

Gamberini et al., 2009), both containing grasping cells (Taira et al., 1990; Raos et al., 2004), V6A has the necessary functional properties and anatomical connectivity to support, in principle, the integration of visual and motor signals needed for visual guidance of prehension. In other words, V6A can be assigned the role of 'dorsomedial grasping area'. Up to now, V6A grasp-related neurons were studied for natural grasping (Fattori et al., 2004), and in controlled tasks testing different hand orientations (Fattori et al., 2009) and different grip types (Fattori et al., 2010, 2012) in darkness. More recently, it has been demonstrated that the modulation of V6A grasping activity by wrist orientation is deeply influenced by visual feed-back (Breveglieri et al., 2016) however, the effect of visual feed-back on modulation of V6A grasping activity by grip type has never been tested .

The main purpose of the present work was to analyze the interplay between grip type and visual information in V6A cells, using a paradigm with several objects of different shapes (requiring different grip types) and different visual backgrounds. Moreover, we compared V6A grasping responses with grasping responses of area AIP studied in similar experimental conditions (Murata et al., 2000). We also studied the grasp-related properties of V6A cells using the same paradigm designed for AIP by Baumann and coworkers (2009) and Schaffelhofer and Scherberger (2016) in order to compare the grip preference and temporal evolution of neural discharges from object vision to grasp performance between V6A and AIP.

Materials and Methods

Experimental procedures

The study was performed in accordance with the guidelines of EU Directives (EU 116-92; EU 63-2010) and Italian national law (D.L. 116-92, D.L. 26-2014) on the use of animals in scientific research. During training and recording sessions, particular attention was paid to any behavioral and clinical sign of pain or distress.

Two male *Macaca fascicularis*, weighing 2.5-4.0 kg, were trained to perform a Reach-to-Grasp task and an Observation task under controlled conditions.

Behavioral tasks

The monkey was seated in a primate chair (Crist Instrument) with the head fixed, in front of a box containing a PC-controlled rotating carousel subdivided into five sectors, each containing a different object presented one at a time, in a random order.

A variety of objects of different shapes were used (fig. 1A). The types of grip evoked by the various objects changed according to their physical characteristics. The two monkeys used identical hand postures for grasping the same objects and the overall similarity of the grips performed by the two monkeys was confirmed by comparing the video images of their hand postures during grasping. The objects and the grip types used for grasping them (fig. 1A) are as follows: “ball” (diameter: 30 mm) grasped with *whole-hand prehension*, with all the fingers wrapped around the object and with the palm in contact with it; “handle” (thickness, 2 mm; width, 34 mm; depth, 13 mm; gap dimensions, 2x28x11 mm) grasped with *finger prehension*, all fingers except the thumb inserted into the gap; “ring” (external diameter, 17 mm; internal diameter, 12 mm) grasped with the *hook grip*, the index finger was inserted into the hole of the object; “plate” (thickness, 4 mm; width, 30 mm; length, 14 mm) grasped with the *primitive precision grip,* using the thumb and the distal phalanges of the other

fingers; “cylinder-in-groove” (cylinder with base diameter of 10 mm and length of 11 mm, in a slot 12 mm wide, 15 mm deep, and 30 mm long) grasped with the *advanced precision grip*, with the pulpar surface of the last phalanx of the index finger opposed to the pulpar surface of the last phalanx of the thumb.

The object selected for each trial was set up by a PC-controlled rotation of the carousel during the intertrial period. Only the selected object was visible in each trial; the view of the other objects was occluded. The objects were always presented in the same spatial position (22.5 cm away from the animal, in the midsagittal plane).

Animals performed two tasks: 1) Reach-to-Grasp in the light (“visually-guided”, Fig. 1B) and in darkness (“memory-guided”, Fig. 1B), and 2) Observation task, where no reach-to-grasp movement was required or performed (Fig. 1C). All tasks began when the monkey pressed a “home” button (2.5 cm in diameter, placed outside the animal’s field of view, 5 cm in front of the chest, on the animal's midsagittal line), in complete darkness (fig. 1B, C). After button pressing, the animal awaited instructions in darkness (*Free*). It was free to look around, though remaining in darkness. After 0.5-1 s, the fixation LED (masked by a 1.5 mm aperture: fixation point) lit up and the monkey had to fixate on it. After a fixation period of 0.5–1 s *(Fixation)*, two white lateral LEDs were turned on and the object was illuminated (circular area of 8 cm diameter with the object in the center) for a period of 0.5 s (*View*). These events were common to all tasks; the object presentation was the cue for all subsequent events as it instructed the animal which object should be grasped.

The two tasks diverged after these events. In the *Reach-to-Grasp* task in the light, the lights on the objects stayed on and the animal could perform visually-guided reach, grasp and hold actions. In the Reach-to-Grasp task in darkness, the light on the object turned off and the monkey had to remember the required action properly. In the dark condition, the brightness of the fixation point was reduced so that it was barely visible during the task: standing by the monkey, the experimenter could not see the object or the monkey’s hand moving in the peripersonal space, even after an adaptation period. Thus, in this condition we have to exclude the possibility that the cell's modulation during grasp

preparation, execution, and object holding could be the consequence of visual stimulation evoked by the vision of the arm moving in the visual field. Despite these differences, the timeline of the two conditions of the Reach-to-Grasp task was the same: after a delay period of 1-1.5 s, during which the monkey was required to maintain fixation on the fixation point without releasing the home button (*Delay*), the color of the fixation point changed. This was the go-signal for the monkey to release the button and perform a Reach-to-Grasp movement (*Mov*) to reach and grasp the object, pull it and keep holding it (*Hold*) till the fixation point switched off (after 0.8-1.2 s). The fixation point switch-off cued the monkey to release the object (*Return*) and to press the home-button again. Home-button pressing ended the trial, allowed the monkey to receive its reward, and started another trial (*Free*) in which another object, randomly chosen, was presented.

In the *Observation* task (Fig. 1C), after 1s of object illumination, a color change of the fixation point (from green to red, *Go*) instructed the monkey to release the home button. The lights illuminating the object were then turned off and monkey could break fixation, receiving its reward. Reach and grasp actions were not required in this task, and a door at the front of the chair blocked hand access to the object.

All tasks (Reach-to-grasp tasks in the light and in the dark, and Observation task) were performed in separate blocks. In each task, five objects were presented 10 times each in random order in a block of 50 correct trials. The animal learned that the presence of the blocking door at the beginning of the block meant that arm movement was not required. After some training sessions in which the animal tried to perform the arm movement anyway, and was not rewarded, it learned not to move the arm during the Observation task. The purpose of this 'no reach/no grasp condition' was to change the context of the visual cue from one of motor behavior (preparation of an appropriate hand posture for grasping) to one of passive object viewing.

During all task conditions, the monkey was required to fixate on the fixation point. If fixation was broken (5°×5° electronic window), trials were interrupted on-line and discarded. The correct performance of movements was monitored by pulses from microswitches (monopolar

microswitches, RS Components, UK) mounted under the home button and the objects. Button/object presses/releases were recorded with 1 ms resolution. For a detailed description of the trial execution control system see (Kutz et al., 2005). Monkeys' arm movements were continuously video-monitored by means of miniature, infrared-illumination-sensitive videocameras.

Surgical and recording procedures

After training completion, a head-restraint system and a recording chamber were surgically implanted in asepsis and under general anesthesia (sodium thiopental, 8 mg/kg/h, *i.v.*) following the procedures reported in Galletti et al. (1995). Adequate measures were taken to minimize pain or discomfort. A full program of postoperative analgesia (ketorolac trometazyn, 1mg/kg, *i.m.,* immediately after surgery, and 1.6 mg/kg, *i.m.*, on the following days) and antibiotic care [Ritardomicina® (benzathine benzylpenicillin + dihydrostreptomycin + streptomycin) 1-1.5 ml/10kg every 5-6 days] followed the surgery.

Single neurons were extracellularly recorded from area V6A of the anterior bank of the parieto-occipital sulcus. We performed single microelectrode penetrations using homemade glass-coated metal microelectrodes, and multiple electrode penetrations using a five-channel multielectrode recording minimatrix (Thomas Recording, GMbH, Giessen, Germany). The recording procedures we used are described in detail in Fattori et al. (2012). Spikes were sampled at 100 KHz and eye position was simultaneously recorded at 500 Hz using an infrared oculometer (Dr. Bouis, Karlsruhe, Germany). Behavioral events were recorded with a resolution of 1 ms.

Histological reconstruction of electrode penetrations was performed as described in detail in other works (Galletti et al., 1999; Gamberini et al., 2011). Briefly, electrode tracks and the approximate location of each recording site were reconstructed on histological sections of the brain on the basis of marking lesions and several other cues, such as the coordinates of penetrations within the recording chamber, the kind of cortical areas passed through before reaching the anterior bank of

the parieto-occipital sulcus and the distance of the recording site from the surface of the hemisphere.

Data analysis

The analyses were performed using custom scripts in Matlab (Mathworks, Natick, MA, US) and SPSS software.

Analysis of the neuronal activity during the Reach-to-Grasp task either in the dark or in the light was made by quantifying the discharge recorded during each trial in the following time epochs (Fig. 1B):

- *FREE*: from home button pressing to the illumination of the fixation LED. This 0.5-1s period of darkness, when gaze was unrestricted, was used to calculate baseline firing when categorizing V6A neurons as Visuomotor, Visual, or Motor, as performed by Murata in AIP (Murata et al., 1996).
- *FIX*: the first 500 ms of gaze fixation on the fixation LED. Firing rates during this interval were used as the reference value for statistical comparison to subsequent task epochs to determine the task-related population.
- *VISG:* response to object presentation, from 40 ms after object illumination to 300 ms after it (total duration: 260 ms).
- *DELAY*: the last 500 ms before the go-signal. It contains the cell discharge during arm movement preparation.
- *MOV*: from 200 ms before movement onset (home-button release) to movement end (object pulling). It contains the discharge of the cell during grasping execution.
- *HOLD*: from object pulling to 200 ms before the onset of return movement (object release). It contains the discharge of the cell during object holding.

For the Observation task (Fig. 1C):

- *FREE*: from home button pressing to the illumination of the fixation LED.
- *VIS*: transient response to object presentation, from 40 ms after object illumination to 300 ms after it (total duration: 260 ms).
- *LONGVIS*: sustained response to object presentation, from 40 ms after object illumination to 1000 ms after it (total duration: 960 ms).

The epochs quantifying visual responses to object illumination (VISG, VIS and LONGVIS) start at 40 ms because visual responses in V6A have a delay of this order (Kutz et al., 2003).

We analyzed only those units tested in at least 7 trials for each object/grip. The reasons for these conservative criteria are dictated by the intrinsic high variability of biological responses (Kutz et al., 2003).

We performed a 3-way ANOVA (factor1: epoch - FIX, DELAY, MOV, HOLD; factor2: objects - 5 levels, one for each objects tested; factor3: visual condition - dark, light) on all the recorded cells. Task-related cells were defined as cells with a significant epoch effect followed by a significant difference between FIX and at least one of the epochs DELAY, MOV, HOLD (post-hoc comparisons, $p<0.05$, Bonferroni corrected for multiple comparisons). FIX was chosen as a reference because in this epoch no visual stimuli were present, the animal's gaze was still, and the monkey was not executing or preparing any arm movement. Task-related cells were further analyzed.

Significant modulation of neural activity by the grip type or visual task conditions was studied by a two-way ANOVA (factor 1: object (5 levels, one for each objects tested); factor 2: visual condition (2 levels, light, dark); $p<0.01$) in each task epoch (Fig. 2A).

In addition, tuning significance for grip type and visual condition was tested at multiple time points *t* using a two-way ANOVA on the spike count in a 200 ms window centered around *t*. This test was repeated in time steps of 50 ms (sliding window ANOVA, fig. 2B). Criteria for significant tuning were the same as for the ANOVA analysis of the fixed time epochs. For the purpose of comparison

of V6A data with AIP in the same analytical conditions, we also repeated the sliding ANOVA in time steps of 1ms (Fig. 8A).

Population responses of tested neurons were computed as average spike density functions (SDFs). An SDF was calculated (Gaussian kernel, half-width 40 ms) for each neuron included in the analysis. SDF was averaged across all trials for each tested grip, separately for light and dark conditions. We found the peak discharge rate of the neuron during the epoch of interest, and used it to normalize SDF. The normalized SDFs were then averaged to derive population responses (see Marzocchi et al. 2008). We statistically compared the population SDFs in dark and light conditions with a permutation test (10,000 iterations) comparing the sum of squared errors of the actual and randomly permuted data. We ran the permutation test in the epochs VISG, DELAY, MOV and HOLD, as already defined. In the permutation test, post-hoc comparisons were performed, thus correcting for multiple comparisons.

We also performed demixed principal component analysis (dPCA, for details see Kobak et al. 2016), by the free code available at: http://github.com/machenslab/dPCA. In contrast to PCA, dPCA reduces the dimensionality of the data, taking task parameters (i.e., sensory and motor variables controlled or monitored by the experimenter) into account. Consequently, this technique avoids mixed selectivity from remaining in the data even after the dimensionality reduction step, impeding interpretation of the results. Thus, the most important advantage of dPCA, compared to standard PCA, is that each component does not show mixed selectivity, but they result 'demixed'. This demixing simplifies exploration and interpretation of neural data, as shown by Kobak and collaborators (Kobak et al., 2016). The time courses of dPCA signals were compared by a permutation test (see Fattori et al. 2010).

Results

To study the contribution of visual feedback and hand shaping on the activity of V6A neurons during grasping of three-dimensional, graspable objects, we employed a Reach-to-Grasp task in which the monkeys reached to and grasped objects of different shapes in the dark and in the light (Fig. 1B). In both visual conditions, the Reach-to-Grasp task required the monkey to move its hand from a position near the body to a fixed position in the peripersonal space where the object was presented. In the task performed in the dark, the object had to be grasped in darkness after a brief visual presentation. In the task performed in the light, the object and the working space were illuminated during grasping preparation, execution, and object holding. Each trial randomly presented one of 5 objects shown in Fig. 1A. Each object was grasped with a distinct hand posture (Fig. 1A), allowing us to equate object shape to hand grip.

Single-unit activity was recorded from 317 neurons of area V6A in two monkeys (case 1, N=134; case 2, N=183). Results were consistent between animals (Chi-squared test, $p>0.05$), and are thus presented jointly. A three-way ANOVA was used to assess whether a cell was task-related (see Materials and Methods). Epochs of interest were: 1) movement preparation (epoch DELAY, the last 500 ms before the instruction signal to Reach-to-Grasp the object), 2) grasping execution (epoch MOV, from 200 ms before the movement onset to movement end) and 3) object holding (epoch HOLD, from the onset of object holding to 200 ms before the return movement onset). 276 of the 317 recorded cells (87%) showed task-related activity.

Furthermore, two-way ANOVA analysis ($p<0.01$) revealed that both visual condition (dark vs light) and grip type (specific object shape) significantly influenced the firing rates of the majority of task-related neurons in each of the three epochs (Fig. 2A, VISUAL CONDITION&GRIP). 41% of the task-related cells were modulated during grasping preparation (DELAY), 59-60% during movement execution (MOV) and object holding (HOLD). The individual factors (VISUAL CONDITION or GRIP) influenced only a minority of V6A cells (about 10-20% depending on the epoch).

To investigate the tuning for grip type and visual condition over time, without constraining the analysis to fixed epochs, we extended the 2-way ANOVA on a sliding window approach (width: 200 ms, step: 50 ms). As shown in Fig. 2B, this analysis revealed that, right after object illumination and after movement onset, the percentage of cells modulated by grip was higher than the percentage of cells modulated by visual condition. During DELAY, before movement execution, the influence of the two factors was similar.

Visual, Motor and Visuomotor cells

We divided V6A neurons modulated in MOV (N=238) into three categories (Visuomotor, Visual, and Motor) based on firing rates during the MOV epoch during visually and memory guided trials in the light and dark, respectively. Murata and collaborators used the same classification scheme to study AIP (Murata et al., 2000), thus enabling a direct comparison of V6A with AIP neurons. Visuomotor neurons had different grasp-related firing rates in the light and the dark, and both rates were significantly higher than the responses in the baseline interval (FREE). Visual neurons showed grasp-related firing in the light but not in the dark. Motor neurons fired at similar rates in the light and the dark during grasping. A total of 39% were Visuomotor cells (N= 92/238), 31% were Visual cells (N= 74/238), and 30% were Motor cells (N=72/238).

Those Visual and Visuomotor neurons that were also tested with the Observation task (N=125) were further subdivided into two classes similarly to what was reported for AIP neurons (Taira et al., 1990; Sakata et al., 1995; Murata et al., 2000): 'Object-type' neurons, if the neurons also responded to the passive vision of the object in the Observation task (Student's t-test between FREE and VIS, $p<0.05$) without any possibility to grasp it; 'Nonobject-type' neurons, if they did not respond to the passive vision of the object ($p>0.05$). We found that the majority of Visual and Visuomotor neurons were *Object-type* (N= 76/125, 61%). The remaining 59 cells were Motor cells and were not further subdivided, as done in AIP (Murata et al. 2000).

A neuron was classified as 'Visual' if its discharge during MOV was significantly higher than the discharge during FREE in the light but not in the dark (Student's t-test, $p<0.05$). The cell shown in Figure 3A is an example of Visual neuron. The activity was on average higher in light than in dark conditions. The neuron discharged strongly during the vision of the object (V in the figure) and during the execution of Reach-to-Grasp actions (M) in the light, with a preference for advanced precision grip and whole-hand prehension (1st and 3rd panels). This cell discharged weakly (or not at all) for the other three grasps. No activations were present, even in the light, during DELAY. The stronger responses during grasping observed only in the light and in MOV were likely caused by the vision of the hand approaching and grasping the objects. The fact that this response in the light occurred after the hand has left the home button (second alignment) corroborates a visually driven explanation of this discharge. This view is also supported by the fact that the 2 preferred actions did not share anything from the point of view of motor control, the advanced precision grip and the whole hand prehension being at the 2 extremes of grasping difficulty. Interestingly, the cell response during object observation is different in the dark and in the light, as reported for the population discharge (Fig. 5A left, see below).

A neuron was classified as 'Motor' if its discharge during MOV: i) was significantly different with respect to the discharge during FREE in both the dark and the light (Student's t-test, $p<0.05$) and ii) was similar in the dark and in the light (Student's t-test, $p>0.05$). In these cells, adding the visual information did not consistently modify the discharge during grasping execution. The cell in Figure 3B is a Motor neuron. This cell fired strongly for grasping all the objects tested, with a preference for grasping the handle and the plate (2nd and 4th panels), that share a flat shape. The lack of effect of the light upon the grasp-related discharge led us to suggest that a tactile or proprioceptive input from the arm (known to affect V6A discharges, Breveglieri et al. 2002; Gamberini et al. 2011) (Fattori et al., 2017) or an efference copy of the motor command (justified by the demonstrated anatomical input of the dorsal premotor cortex to V6A; Shipp et al. 1998; Gamberini et al. 2009) may be responsible for this discharge during grasping.

A neuron was classified as 'Visuomotor' if its discharge during MOV: i) was significantly different with respect to the discharge during FREE in the dark, or in both the dark and the light (Student's t-test, $p<0.05$) and ii) was different between the dark and the light (Student's t-test, $p<0.05$). Fig. 4 shows two examples of Visuomotor cells, the most represented class of grasping cells in V6A. Figure 4A and B reports an example of Visuomotor 'Object-type' neuron. This cell was strongly activated during preparation and execution of grasping both in light and in dark conditions, although it discharged more in the light (Student's t-test, $p<0.05$, fig. 4A). The cell showed a clear grip sensitivity, discharging more strongly for the preparation and execution of finger prehension, whole-hand prehension and primitive precision grips (2^{nd}, 3^{rd} and 4^{th} panels). It is worth noting that also the DELAY activity (D in the figure) of this cell was modulated consistently with grasping activity.

During the Observation task (fig. 4B), the response to the object presentation ('V' in the figure) was consistent with the visual response shown by the cell in the grasping task: strongest response for observation of the handle, weakest for the cylinder in the groove. This cell also showed a sustained visual response (LV) coherent with the transient visual response (V). This sustained visual response that follows the brisk response to object presentation may reflect object affordance (Fattori et al., 2012)(Breveglieri et al., 2015). In other words, we suggest that V6A Visuomotor cells encode visuomotor parameters even when an explicit motor activation is not required. The fact that the activity in the DELAY is tuned according to the grasping sensitivity but is different in the light and in the dark suggests that the cell receives somatosensory/motor-related and visual information. In summary, this Visuomotor cell was modulated by grasping in the dark, by hand-object vision, and by object observation outside the grasping context.

Figure 4C, D shows an example of Visuomotor Nonobject-type neuron. In the Reach-to-Grasp task (Fig. 4C) the activity of this cell was not tuned for objects during grasping preparation (D). It was tuned during grasping execution (M), showing very low grip sensitivity and higher activity in light conditions no matter what type the grasping was. In the Observation task (fig. 4D), this cell was not

activated during viewing of any object, showing neither a transient (V) nor a sustained (LV) visual response. In summary, this neuron was sensitive to information related to the arm movement and to visual information related to the occurrence of the grasping, but it was not sensitive to the visual features or affordance of the object to be grasped.

To examine whether and to what extent visual feed-back affected the activity of Visual, Motor, and Visuomotor neurons, we calculated the average normalized SDFs for each visual condition, separately for the different classes. They are illustrated in Figure 5. As expected, Visuomotor neurons (fig. 5A, left panel) discharged significantly more in the light than in the dark for all the epochs of interest (permutation test, $p<0.05$),including object presentation (VISG). Visual cells (fig. 5B, left panel) showed stronger activity in the light than in the dark in all the epochs considered (permutation test for DELAY, MOV and HOLD, $p<0.05$). It is worth noting that in the light these cells had a stronger discharge also at object presentation (permutation test, $p<0.05$), though the visual stimulation was the same as in dark condition (see fig. 1B).

The Motor neurons (fig. 5C) showed activities that were not significantly different in light and dark conditions in all epochs considered (permutation test, n.s., $p>0.05$). The small peak of activity recorded at object presentation before grasping (VISG) in light and in dark conditions (significantly different from the baseline activity, permutation test $p<0.05$) prompted us to check how many Motor neurons showed this 'visual' response. We found a complex frame. Some Motor neurons were responsive to object illumination (VISG) in the Reach-to-grasp task in the dark (44%), and 28% in the Reach-to-grasp task in the light. The remaining 56% of Motor cells were not responsive during VISG in the dark, and 72% in the light.

To better define these unexpected 'visual' responses of Motor neurons to object presentation, we compared the response to object presentation before the grasp (VISG) with the response to object presentation in the observation task (VIS): 39% of Motor cells did not respond to object presentation either in the Reach-to-grasp task (VISG) or in the Observation task (VIS), thus confirming their complete motor/somatosensory nature. Another portion of Motor cells (28%)

showed a significant response to object illumination both in the Reach-to-grasp task (VISG, t-test, $p<0.05$) and in the Observation task (VIS, t-test, $p<0.05$), suggesting that they received visual information on the observed object. Finally 33% of Motor neurons showed a response to object illumination only in the Observation task (VIS), indicating a possible context-dependent discharge, as discussed below.

Relative weight of visual information and grip type on neuronal modulation

Area V6A is known to encode multiple factors related to the control of prehension (see for a review Fattori et al. 2015). In the current study, we employed a task where multiple objects and two visual conditions were used, increasing potential confounds in the interpretation of the data. To represent the main factors influencing the neural population, we used the demixed principal component analysis (dPCA, see Kobak et al. 2016), a dimensionality reduction method for extracting low-dimensional linear combinations of a population that represents specific task features. Figure 6 shows the results of dPCA of task-related units. As shown in figure 6A, the amount of variance explained by dPCA was very similar to that extracted by classical PCA, suggesting that the dPCA method can properly extract the most relevant task features from our population of cells. The principal dPCA component explaining the most variance overall was a condition-independent signal (Figure 6B) that begins right before the movement onset, as shown by the analysis of its time course (fig. 6C). This component may reflect signals present in V6A and common to all the conditions tested in this task design. An example of a condition-independent signal may be related to the transport phase of the arm movements performed in the current task, as it is well known that reaching signals do influence V6A cells (Fattori et al., 2005; Hadjidimitrakis et al., 2014). In any case, the variance captured by the condition-independent variable is present in other neurophysiological data (see Kobak et al. 2016); indeed in our case the influence of the condition-independent signal was lower.

Interestingly, grip type represented an important component (31%, Fig. 6B). The timing of the first component of grip type (Component #4, fig. 6D) revealed that the components of grip types were well separated from movement planning up to grasping execution, with the highest separation at the end of delay and onset of grasping execution. In addition, the signal related to the handle grasping was separated from the other signals during grasping preparation and execution (permutation test, $p<0.05$), but not during object holding where all the curves converge. The dPCA also shows the low influence of visual information (14%, fig. 6B). The timing of this signal shows that light and dark signals were well separated for the entire task, since the beginning of the delay (fig. 6E).

Comparison with AIP

To better identify whether V6A plays similar or different functional roles with respect to the classic PPC grasping area AIP, we compared our results with those obtained by other labs on AIP (Murata et al., 2000; Baumann et al., 2009; Schaffelhofer and Scherberger, 2016), using the same experimental design and analyses.

The results of the comparison (fig. 7A) showed that the incidence of Visual, Motor, and Visuomotor cells (Object- and Nonobject-type) was statistically not different in areas V6A and AIP (Chi-squared test, $p>0.05$). To examine whether Visual, Motor, and Visuomotor neurons exhibit a grip selectivity similar to that reported by Murata and collaborators in AIP (Murata et al., 2000), thus enabling a direct comparison of V6A with AIP, we analyzed the activity of neurons during MOV when grasping the five objects in the light. In agreement with the analysis performed by Murata et al. (2000) in AIP, we excluded those neurons that were not studied with the Observation task and those neurons that were not tuned by grip type (1-way ANOVA, $p>0.05$). The remaining 140 Visual, Motor, and Visuomotor neurons were further subdivided according to their degree of selectivity for the objects (the Student-Bonferroni procedure, 2-tail; $p<0.01$). We classified them as *highly selective*, when the activity of the neurons for one object was significantly higher than that

for all the other objects, or *moderately selective*, when, despite the cells being tuned for objects according to ANOVA, not all the posthoc comparisons were significant (Student-Bonferroni procedure, n.s.). The remaining neurons that did not show any significant difference in the activity level for the five objects were classified as *nonselective* (Student-Bonferroni procedure, n.s.). To evaluate the selectivity for the passive observation of the object, we performed the same analysis considering the discharge during the epochs VIS and LONGVIS in the Observation task (the Student-Bonferroni procedure, 2-tail; $p<0.01$). The selectivity for 'active' object observation (observation in the Reach-to-Grasp task) was evaluated using epoch VISG.

As shown in Figure 7B, C, the distribution of V6A and AIP cells based on their selectivity was similar in the two areas (Chi-squared test, $p>0.05$). Considering all neuronal categories together (fig. 7 B and C), the incidence of highly selective cells (38%) was slightly smaller than that of moderately selective cells (44%) in V6A, a result similar to AIP.

The most interesting result regarding the cell categories is related to the selectivity of these cells for objects observed in the Observation task (Table 1). The discharge for passive object observation was nonselective in the overwhelming majority of Object-type cells (about 80% VIS, see Table 1), whereas in the Reach-to-Grasp task the active vision of the object (VISG) gave rise to a higher incidence of selective (highly or moderately) neurons. In other words, most of the cells significantly tuned for object presentation during grasping in the light lost their object selectivity when simply observing the object without any grasping preparation.

To make a direct comparison with AIP, we have to take into account the late, sustained part of the visual response to object observation (LONGVIS), as done by Murata (Murata et al., 2000). Doing this (Table 1), the selectivity in V6A Visual Object neurons increases to 53%, similarly to AIP (at least 57%, (Murata et al., 2000); in contrast, the percentage of selective neurons among V6A Visuomotor category is 43%, much less than those in AIP (at least 81%; Murata et al., 2000).

Differently from AIP (Murata et al., 2000), not only were there very few neurons in V6A selective for objects in the Reach-to-Grasp and Observation tasks , but also in just a minority of them (3/11 in

VIS and 12/29 in LONGVIS) there was the same object preference between object observation and grasping. Consistency was, instead, a rule for AIP (Murata et al., 2000).

To further compare the contribution of AIP and V6A to grasp encoding, we evaluated the incidence of grip tuned cells in the two areas. For the sake of comparison, we used only V6A data recorded in the dark and AIP data recorded with the set of objects (called "mixed objects") of Schaffelhofer and Scherberger (2016) more similar to ours, so as to better match the two studies. In addition, we performed the sliding window ANOVA in time steps of 1ms and set the significance level at 0.01, to use the same conditions applied by Schaffelhofer and Scherberger (2016) in AIP. The comparison is shown in figure 8A: during object illumination, the incidence of grip tuned cells in AIP and V6A was similar (about 40%); during grasping preparation, the incidence of tuned cells decreased in AIP while in V6A it remained more or less constant; during grasping execution, the incidence of grip tuned cells rose to about 60% in V6A while the increase in AIP was much less pronounced. These data show a similar involvement of neural populations in the two areas at the beginning of the trial, when object shape is encoded to drive the subsequent grasping, but later in the trial V6A remains higher when action needs to be launched and monitored inflight.

To perform another direct comparison between the functional properties of V6A and AIP, we analyzed task-related cells of V6A tested in the dark with the same grips (finger prehension and advanced precision grip) used in another study of AIP (Baumann et al., 2009). The results are shown in fig. 8B, C. Fig. 8B shows the ratio of cells preferring precision vs power grip in V6A (top) and AIP (bottom). The ratio was similar (half of the cells preferred precision and half power grip) in VIS, quite similar in DELAY, and clearly different in MOV, where power grip was preferred in V6A and precision grip in AIP.

Fig. 8C shows the changes of preference of individual V6A and AIP cells along the time-course of the task. In V6A, about 40% of the cells changed their preference, passing from VISG to DELAY, whereas about 70% of cells maintained the same preference, passing from DELAY to MOV. In AIP, instead, the tuning preference remained more constant, passing from about 60% between VIS and

DELAY to about 70% between DELAY and MOV. Overall, the distributions of these AIP and V6A data are statistically different (Chi-squared test, $p<0.05$).

Discussion

In this work, we investigated the relative influence of grip type and visual condition of the grasping action on the discharge of neurons in area V6A, a visuomotor area located in the medial PPC. We also compared the functional properties of grasp-related cells of V6A with those of AIP, the grasping area of the lateral PPC. The present study demonstrates that the majority of V6A neurons are modulated by both grip type and visual information, from grasping preparation up to execution and object holding. As shown by the dPCA and sliding window analyses, grip type influences the discharge of V6A cells more than visual information available when grasping is prepared and accomplished. The higher grip-related than visual-related selectivity found in V6A may suggest that, despite its name starting with the letter "V", V6A should not be counted among the extrastriate visual areas, but among the posterior parietal grasping areas.

In our Reach-to-Grasp task, each tested object was grasped with a distinct grip. Thus, grip type is not dissociated from object feature/affordance, and we cannot distinguish which of the two is encoded by the cells. In a previous work, we demonstrated that the response of V6A neurons to the presentation of objects to be grasped does reflect the object affordance (Breveglieri et al., 2015). The present findings suggest that the response to object presentation may include, together with an encoding of the visual attributes of the object and of its affordance, context-dependent factors too. As context-dependent responses have been found in ventrolateral prefrontal cortex and pre-SMA (Bruni et al., 2015)(Simone et al., 2015)(Lanzilotto et al., 2016), which are directly connected to V6A (Gamberini et al., 2009)(Lanzilotto et al., 2016), we speculate that context-dependent information could impinge upon V6A cells and be responsible for at least some of the behavior we observed in the present paper, like the response to object illumination of Motor neurons only in the

Observation task.

This complex visual encoding performed by V6A, together with the influx of attentional shifts on V6A discharges (Galletti et al., 2010; Ciavarro et al., 2013), suggest that V6A provides critical visual and cognitive information to motor structures controlling hand action (see Fattori et al., 2017).

The present data, as well as previous reports from our laboratory (Fattori et al., 2010, 2012), have shown that V6A cells were deeply influenced by grip type during movement execution and object holding. In a recent study measuring hand kinematics during grasping, Schaffelhofer and Scherberger (2016) reported that the first principal component of hand movements could be attributed to wrist orientation and the second principal component to grip aperture. Although there are no doubts that V6A cells encode wrist orientation used for grasping (Fattori et al., 2009; Breveglieri et al., 2016), as all the objects were grasped with a constant wrist orientation in the present task (see figure 1A), one would expect more convergence of firing rates for the different grasps than is reported here if the cells were *only* modulated by wrist orientation. Actually, the high percentage of cells modulated by grip type (around 70-80%) during grasping execution and object holding suggests that V6A cells are not only modulated by wrist orientation, but also by hand shaping.

This study demonstrates that several V6A neurons are strongly modulated by grip type during DELAY, i.e. during the period in which the monkey withholds the grasping action. This activity could be related to grasping preparation, or, especially in darkness, to the memory of the object to be subsequently grasped. This feature makes V6A similar to premotor area F2 (Raos et al., 2004), and to parietal area AIP, where limited set-related activity and extensive memory-related activity was found (Murata et al. 1996; Schaffelhofer et al. 2015; Schaffelhofer and Scherberger 2016). However, our task does not make it possible to ascertain what is encoded by V6A in the delay between object observation and action execution, because there is a one-to-one conrrespondence between onject shape and grip type. Our previous work with the grasping performed only in the

dark showed that in the delay before grasping, V6A cells started encoding object features and then switched to encoding grip type (see Fig. 8 of Fattori et al., 2012). Further work is needed to disentangle what is encoded in the delay epoch by V6A neurons.

The use of objects with different shapes, that require different grips, allowed us to investigate the presence of Motor, Visual, and Visuomotor neurons, similarly to what has been previously done in AIP (Sakata et al., 1995; Murata et al., 2000). The present data show that V6A contains 30% of Motor cells, 31% of Visual cells, and 39% of Visuomotor neurons. We suggest that, while Visual neurons receive only visual signals, the Visuomotor neurons incorporate both visual and somatosensory/motor efferent copy signals and integrate them in guiding prehension. The Motor neurons do not receive visual information about hand/object interaction, because they show the same response in MOV in the dark and in the light. Some of them, however, may receive visual information about the observed object.

About 40% of the V6A cells were the 'Object-type' because they discharged also on passive observation of the object. The Object-type neurons likely represent visual physical characteristics of the objects. However, since in V6A the object selectivity of this type of neuron found when the monkey observed the objects at the beginning of the grasping trials was reduced during passive object observation (i.e., observation outside the grasping context), we believe that these neurons did not encode the visual features of the objects, useful for object recognition. We suggest, instead, that they encoded the visual information useful for the subsequent grasping action (the visual affordance; Breveglieri et al., 2015). The 'Nonobject-type' neurons are influenced by visual information only during movement execution – not before - (see fig. 5) and this could be useful for the online control of reach-to-grasp movements, including the adjustment of grip around the object.

The discharge stronger in the light than in the dark conditions in Visual and Visuomotor cells deserves some considerations. As pointed out above, it is worth noting that before and at object presentation the visual stimulation was the same in the two visual conditions (View, see fig. 1B). Thus, what is the reason for a stronger discharge in the light? The fact that the phenomenon is

present in Object-type but not in Nonobject-type cells (fig 5A and B, center and right panels) excludes the possibility that it is caused by the block design. Interestingly, while Nonobject-type neurons show a significant difference only during the execution of grasping action, Object-type neurons start differentiating the discharge between light and dark conditions at object vision, and continue through the delay up to grasping execution. Since in the dark, monkeys had to memorize the object to be grasped and likely had to pay more attention because they knew that the information about the object would not be available for the rest of the trial, it could be that the difference in discharge in the two conditions is due to the attentional level, with an inhibitory effect tied to the attentional enhancement. This view is supported by the report that many V6A neurons are inhibited when the animal starts to work in a fixation task (see Fig. 16 in Galletti, 1996).

As an alternative explanation, it could be that a higher likelihood of shifts of attention in the light compared to the dark may be responsible for the higher activity we observed in the light. In support of this attentional shift hypothesis is the report that V6A activity is strongly modulated by the shifts of attention (Galletti et al., 2010; Ciavarro et al., 2013), a finding recently confirmed by Caspari et al (Caspari et al., 2015).

The dPCA analysis of the present data allowed us to measure the relative influence of visual information and of grip type. We found that the influence of visual information in V6A is quite weak (14%), and lower than the influence of grip type (31%, see fig. 6B). This result is surprising, given that the majority of V6A cells are visual neurons (Galletti et al., 1999; Fattori et al., 2017). However, this might have some functional explanations. For example, in humans it has been demonstrated that the impact of a specific source of sensory information (visual, haptic) on the sensorimotor transformation is regulated to satisfy task requirements (Säfström and Edin, 2004). Since in our experiments the animals were overtrained to perform Reach-to-Grasp tasks in light and in dark conditions, the visual information available during grasping in light was not necessary to allow task completion. Hence, the neural modulations we observed in V6A during grasping could be strictly tied to the strong somatosensory/motor activities because they are behaviorally relevant

in our conditions. Further, specific experiments are needed to confirm this suggestion.

Medial versus lateral parietal grasping areas

The use of the same experimental protocol used in AIP studies allowed us to compare the grasping properties of the lateral parietal area AIP with those of the medial parietal area V6A. In a comparison with Sakata's work, V6A shows a similar incidence of grasp-related cells with respect to AIP (78% vs. 67%, Taira et al. 1990). In a direct comparison of the current results with those of Scherberger and coworkers, it emerges that at the object presentation V6A and AIP recruit a similar amount of cells (see Fig. 8A), whereas during the subsequent grasping preparation and execution V6A seems to recruit more cells than AIP. Of course, this comparison is only suggestive, as the data come from different laboratories and from different recording apparatuses (chronic arrays for AIP, vs single electrodes for V6A). However, a possible explanation for the higher incidence of grasp-related cells in V6A could be the presence of somatosensory cells in this area, but not in AIP (Murata et al., 2000; Breveglieri et al., 2002). Somatosensory cells related to the arm (as they are in V6A; Breveglieri et al. 2002) fire immediately before arm movement, when the muscles start contracting, and during reach-to-grasp execution and hand-object interaction.

The incidence of Visual, Motor, and Visuomotor neurons, as well as that of Object and Nonobject-type neurons is similar in V6A and AIP (see fig. 7A) (Sakata et al., 1995; Murata et al., 1996, 2000). However, the discharge of the subset of V6A Motor neurons at object presentation is different from that of AIP motor neurons, that '..were not activated during the fixation period of the manipulation task in the light…' (Murata et al., 2000). For all the other aspects, the three classes of neurons were similar between V6A and AIP. Moreover, the grip selectivity in the two parietal grasping areas turned out to be remarkably similar. The distribution of highly selective, moderately selective, and nonselective cells was similar in the two areas (see fig. 7B, C). However, most of the AIP neurons (at least 81% of the Visuomotor Object-type cells and at least 57% of the Visual

Object-type cells) were selective for grips during manipulation task and for objects during passive object observation (Murata et al., 2000). On the contrary, only a minority of V6A neurons did so. Thus, it seems that while both visual and motor components do influence the selectivity of Visual and Visuomotor cells in AIP, in V6A it is the motor component that particularly drives a cell's selectivity, a view strongly supported by the results of dPCA analysis, as recalled above (see fig. 6). At individual cell level, AIP showed high consistency of object preference between visual presentation of the object and its grasping, whereas in V6A this consistency was poor. This lack of consistency in V6A may reflect contextual information and/or attentional signals, summing up with the visual and motor-related ones that largely impinge on V6A. At population level, the number of V6A cells modulated in the delay before action and in grasping execution is higher than in AIP (see fig. 8A). This, together with the rich direct connections between V6A and MIP and dorsal premotor cortex (Gamberini et al., 2009), and the high incidence in V6A of neurons processing spatial signals for reaching (Fattori et al., 2005, 2017; Hadjidimitrakis et al., 2014), suggests a deeper involvement of V6A in linking object information to the orchestration of reaching and grasping actions.

Previous experiments demonstrated that about 90% of AIP neurons were sensitive to simple visual stimuli, like fragments of shapes (Romero et al., 2014), whereas only about 30% of V6A neurons were sensitive to simple visual stimuli (Galletti et al., 1999; Gamberini et al., 2011). This difference in visual sensitivity between the two grasping areas has been recently confirmed by reporting a stronger influence of object shape in AIP than in V6A (35% in AIP, Schaffelhofer and Scherberger 2016, versus 25% in V6A, Fattori et al. 2012). Both areas are sensitive to wrist orientation in a similar manner (around 50%, Baumann et al. 2009; Fattori et al. 2009), while, a marked difference between them is evident in the somatosensory domain: somatosensory cells were not found in AIP (Murata et al., 2000), whereas V6A contains about 30% of somatosensory cells (Breveglieri et al., 2002). Thus, AIP seems to be more visually driven than V6A, which instead is more influenced by somatosensory/motor inputs such as the hand posture used for grasping. This different balance of sensory sensitivity in the two areas is in agreement with their different pattern of cortical inputs,

with AIP receiving inputs from the ventral visual stream and the dorso-lateral fronto-parietal network (Borra et al., 2008), and V6A from the extrastriate cortex, the superior parietal lobule and the mesial parietal cortex, but not receiving a direct input from the ventral stream (Gamberini et al., 2009; Passarelli et al., 2011).

A further difference between the two grasping areas concerns the population preference for grips during grasping performance. When precision grip and power grip are compared, AIP showed an over-preference for precision grip (Baumann et al., 2009), V6A for power grip (fig. 8B). This difference likely reflects a different functional role of the two grasping areas, with AIP more involved in manipulation and V6A in secure grasping of objects also in dynamic conditions (Galletti and Fattori, 2017). However, this proposed difference between the two grasping parietal areas should not be considered as a dichotomy but as a concurrent involvement in controlling grasping, because V6A and AIP are also reciprocally connected (Borra et al., 2008; Gamberini et al., 2009) and share many grasp-related properties, as shown here. This proposed interplay between the medial and lateral grasping areas is in line with recent brain imaging work in humans (Di Bono et al., 2015; Fabbri et al., 2016). Together, the dorsomedial parieto-frontal stream involving V6A and dorsal premotor cortex and the dorsolateral stream involving AIP and ventral premotor cortex can cooperate in orchestrating how to approach an object to be grasped in the most appropriate way, according to the type of object and also to the context in which the grasping needs to be accomplished (see also Galletti and Fattori, 2017 for a discussion on this topic).

Conclusions

The present results demonstrate that parietal area V6A is modulated by visual information available during the execution of prehension and grip type, with this latter representing the most influencing factor. The activity modulation changes during the trial, from object presentation up to action preparation and execution, with an evolution indicating that V6A processes vision for action, taking

into account also attentional signals and contextual information (Fattori et al., 2017). This functional role well suits the characteristics of the dorsal visual stream of which V6A is an important node (Galletti et al., 2003; Galletti and Fattori, 2017).

These results also reveal that area V6A shares many features with the other grasp-related parietal area AIP, that allow both areas to integrate visual and motor information to orchestrate grasping actions. AIP seems to be more involved in fine control of precision grip and manipulation, V6A in fast, coarser control of object grasping and in directing the hand to the correct spatial position of the object (Fattori et al., 2017)(Galletti and Fattori, 2017). A possible role for V6A may be to orchestrate the coordination between reaching and grasping so as to contribute to the control of the entire prehension.

Acknowledgements

This work was supported by EU FP7-IST-217077-EYESHOTS, by Ministero dell'Università e della Ricerca (Italy, FIRB2013 prot. RBFR132BKP), and by Fondazione del Monte di Bologna e Ravenna (Italy). We thank Michela Gamberini and Lauretta Passarelli for the anatomical reconstructions and Massimo Verdosci and Francesco Campisi for technical assistance.

References

Baumann MA, Fluet M-CC, Scherberger H (2009) Context-specific grasp movement representation in the macaque anterior intraparietal area. J Neurosci 29:6436–6448.

Borra E, Belmalih A, Calzavara R, Gerbella M, Murata A, Rozzi S, Luppino G (2008) Cortical connections of the macaque anterior intraparietal (AIP) area. Cereb Cortex 18:1094–1111.

Breveglieri R, Bosco A, Galletti C, Passarelli L, Fattori P (2016) Neural activity in the medial parietal area V6A while grasping with or without visual feedback. Sci Rep 6:28893.

Breveglieri R, Galletti C, Bosco A, Gamberini M, Fattori P (2015) Object affordance modulates visual responses in the macaque medial posterior parietal cortex. J Cogn Neurosci 27:1447–1455.

Breveglieri R, Kutz DF, Fattori P, Gamberini M, Galletti C (2002) Somatosensory cells in the parieto-occipital area V6A of the macaque. Neuroreport 13:2113–2116.

Bruni S, Giorgetti V, Bonini L, Fogassi L (2015) Processing and Integration of Contextual Information in Monkey Ventrolateral Prefrontal Neurons during Selection and Execution of Goal-Directed Manipulative Actions. J Neurosci 35:11877–11890.

Caspari XN, Janssens T, Mantini XD, Vandenberghe XR, Vanduffel XW (2015) Covert Shifts of Spatial Attention in the Macaque Monkey. J Neurosci 35:7695–7714.

Chen J, Reitzen SD, Kohlenstein JB, Gardner EP (2009) Neural representation of hand kinematics during prehension in posterior parietal cortex of the macaque monkey. J Neurophysiol 102:3310–3328.

Ciavarro M, Ambrosini E, Tosoni A, Committeri G, Fattori P, Galletti C (2013) rTMS of Medial Parieto-occipital Cortex Interferes with Attentional Reorienting during Attention and Reaching Tasks. J Cogn Neurosci:1–10.

Di Bono MG, Begliomini C, Castiello U, Zorzi M (2015) Probing the reaching-grasping network in humans through multivoxel pattern decoding. Brain Behav 5:e00412.

Fabbri S, Stubbs KM, Cusack R, Culham JC (2016) Disentangling Representations of Object and Grasp Properties in the Human Brain. J Neurosci 36:7648–7662.

Fattori P, Breveglieri R, Amoroso K, Galletti C (2004) Evidence for both reaching and grasping activity in the medial parieto-occipital cortex of the macaque. Eur J Neurosci 20:2457–2466.

Fattori P, Breveglieri R, Bosco A, Gamberini M, Galletti C (2017) Vision for Prehension in the Medial Parietal Cortex. Cereb Cortex 27:1149–1163.

Fattori P, Breveglieri R, Marzocchi N, Filippini D, Bosco A, Galletti C (2009) Hand Orientation during Reach-to-Grasp Movements Modulates Neuronal Activity in the Medial Posterior Parietal Area V6A. J Neurosci 29:1928–1936.

Fattori P, Breveglieri R, Raos V, Bosco A, Galletti C (2012) Vision for action in the macaque medial posterior parietal cortex. J Neurosci 32:3221–3234.

Fattori P, Kutz DF, Breveglieri R, Marzocchi N, Galletti C (2005) Spatial tuning of reaching activity in the medial parieto-occipital cortex (area V6A) of macaque monkey. Eur J Neurosci 22:956–972.

Fattori P, Raos V, Breveglieri R, Bosco A, Marzocchi N, Galletti C (2010) The dorsomedial pathway is not just for reaching: grasping neurons in the medial parieto-occipital cortex of the macaque monkey. J Neurosci 30:342–349.

Galletti C, Battaglini PP, Fattori P (1995) Eye position influence on the parieto-occipital area PO (V6) of the macaque monkey. Eur J Neurosci 7:2486–2501.

Galletti C, Breveglieri R, Lappe M, Bosco A, Ciavarro M, Fattori P (2010) Covert shift of attention modulates the ongoing neural activity in a reaching area of the macaque dorsomedial visual stream. PLoS One 5(11):e15078.

Galletti C, Fattori P (2017) The dorsal visual stream revisited: Stable circuits or dynamic pathways? Cortex doi: 10.1016/j.cortex.2017.01.009.

Galletti C, Fattori P, Battaglini PP, Shipp S, Zeki S (1996) Functional demarcation of a border between areas V6 and V6A in the superior parietal gyrus of the macaque monkey. Eur J Neurosci 8:30–52.

Galletti C, Fattori P, Kutz DF, Gamberini M (1999) Brain location and visual topography of cortical area V6A in the macaque monkey. Eur J Neurosci 11:575–582.

Galletti C, Kutz DF, Gamberini M, Breveglieri R, Fattori P (2003) Role of the medial parieto-occipital cortex in the control of reaching and grasping movements. Exp Brain Res 153:158–170.

Gamberini M, Galletti C, Bosco A, Breveglieri R, Fattori P (2011) Is the medial posterior parietal area V6A a single functional area? J Neurosci 31:5145–5157.

Gamberini M, Passarelli L, Fattori P, Zucchelli M, Bakola S, Luppino G, Galletti C (2009) Cortical connections of the visuomotor parietooccipital area V6Ad of the macaque monkey. J Comp Neurol 513:622–642.

Gardner EP, Babu KS, Reitzen SD, Ghosh S, Brown AS, Chen J, Hall AL, Herzlinger MD, Kohlenstein JB, Ro JY (2007) Neurophysiology of Prehension. I. Posterior Parietal Cortex and Object- Oriented Hand Behaviors. J Neurophysiol 97(1):387–406.

Hadjidimitrakis K, Bertozzi F, Breveglieri R, Bosco A, Galletti C, Fattori P (2014a) Common neural substrate for processing depth and direction signals for reaching in the monkey medial posterior parietal cortex. Cereb Cortex 24:1645–1657.

Hadjidimitrakis K, Bertozzi F, Breveglieri R, Bosco A, Galletti C, Fattori P (2014b) Common neural substrate for processing depth and direction signals for reaching in the monkey medial posterior parietal cortex. Cereb Cortex 24:1645–1657.

Janssen P, Scherberger H (2015) Visual Guidance in Control of Grasping. Annu Rev Neurosci 38:69–86.

Jeannerod M, Arbib MA, Rizzolatti G, Sakata H (1995) Grasping objects: the cortical mechanisms of visuomotor transformation. Trends Neurosci 18:314–320.

Kobak D, Brendel W, Constantinidis C, Feierstein CE, Kepecs A, Mainen ZF, Romo R, Qi X, Uchida N, Machens CK (2016) Demixed principal component analysis of neural population data. Elife 5:1–37.

Kutz DF, Fattori P, Gamberini M, Breveglieri R, Galletti C (2003) Early- and late-responding cells to saccadic eye movements in the cortical area V6A of macaque monkey. Exp Brain Res 149:83–95.

Kutz DF, Marzocchi N, Fattori P, Cavalcanti S, Galletti C, Fattori P, Raos V, Breveglieri R, Bosco A, Marzocchi N, Galletti C (2005) Real-Time Supervisor System Based on Trinary Logic to

Control Experiments With Behaving Animals and Humans. J Neurophysiol 93:3674–3686.

Lanzilotto M, Livi A, Maranesi M, Gerbella M, Barz F, Ruther P, Fogassi L, Rizzolatti G, Bonini L (2016) Extending the cortical grasping network: pre-supplementary motor neuron activity during vision and grasping of objects. Cereb Cortex 26(12):4435-4449.

Lehmann SJ, Scherberger H (2013) Reach and gaze representations in macaque parietal and premotor grasp areas. J Neurosci 33:7038–7049.

Maeda K, Ishida H, Nakajima K, Inase M, Murata A (2015) Functional properties of parietal hand manipulation-related neurons and mirror neurons responding to vision of own hand action. J Cogn Neurosci 27:560–572.

Marzocchi N, Breveglieri R, Galletti C, Fattori P (2008) Reaching activity in parietal area V6A of macaque: Eye influence on arm activity or retinocentric coding of reaching movements? Eur J Neurosci 27:775–789.

Matelli M, Govoni P, Galletti C, Kutz DF, Luppino G (1998) Superior area 6 afferents from the superior parietal lobule in the macaque monkey. J Comp Neurol 402:327–352.

Murata a, Gallese V, Luppino G, Kaseda M, Sakata H (2000) Selectivity for the shape, size, and orientation of objects for grasping in neurons of monkey parietal area AIP. J Neurophysiol 83:2580–2601.

Murata A, Gallese V, Kaseda M, Sakata H (1996) Parietal neurons related to memory-guided hand manipulation. J Neurophysiol 75:2180–2186.

Passarelli L, Rosa MGP, Gamberini M, Bakola S, Burman KJ, Fattori P, Galletti C (2011) Cortical Connections of Area V6Av in the Macaque: A Visual-Input Node to the Eye/Hand Coordination System. J Neurosci 31:1790–1801.

Raos V, Umiltá M-A, Gallese V, Fogassi L (2004) Functional properties of grasping-related neurons in the dorsal premotor area F2 of the macaque monkey. J Neurophysiol 92:1990–2002.

Rizzolatti G (1997) NEUROSCIENCE: Enhanced: The Space Around Us. Science (80) 277:190–191.

Rizzolatti G, Matelli M (2003) Two different streams form the dorsal visual system: Anatomy and functions. Exp Brain Res 153:146–157.

Romero MC, Pani P, Janssen P (2014) Coding of shape features in the macaque anterior intraparietal area. J Neurosci 34:4006–4021.

Säfström D, Edin BB (2004) Task Requirements Influence Sensory Integration During Grasping in Humans. Learn Mem 11:356–363.

Sakata H, Taira M, Murata A, Mine S (1995) Neural Mechanisms of Visual Guidance of Hand Action in the Parietal Cortex of the Monkey. Cereb Cortex 5:429–438.

Schaffelhofer S, Agudelo-Toro A, Scherberger H (2015) Decoding a wide range of hand configurations from macaque motor, premotor, and parietal cortices. J Neurosci 35:1068–1081.

Schaffelhofer S, Scherberger H (2016) Object vision to hand action in macaque parietal , premotor , and motor cortices. Elife 5:1–24.

Shipp S, Blanton M, Zeki S (1998) A visuo-somatomotor pathway through superior parietal cortex in the macaque monkey: Cortical connections of areas V6 and V6A. Eur J Neurosci 10:3171–3193.

Simone L, Rozzi S, Bimbi M, Fogassi L (2015) Movement-related activity during goal-directed hand actions in the monkey ventrolateral prefrontal cortex. Eur J Neurosci 42:2882–2894.

Taira M, Mine S, Georgopoulos AP, Murata A, Sakata H (1990) Parietal cortex neurons of the monkey related to the visual guidance of hand movement. Exp Brain Res 83:29–36.

Table 1

Selectivity for objects of visually responsive grasp-related neurons during object viewing with (Reach-to-grasp task) and without grasping (Observation task). For each type, the number and incidence (in brackets) is indicated.

Type of cell	Highly selective	Moderately selective	Nonselective	Total
VIS (Observation task)				
Visuomotor Object	4 (9%)	4 (9%)	36 (82%)	44 (100%)
Visual Object	1 (5%)	2 (11%)	16 (84%)	19 (100%)
LONGVIS (Observation task)				
Visuomotor Object	9 (20%)	10 (23%)	25 (57%)	44 (100%)
Visual Object	3 (16%)	7 (37%)	8 (47%)	19 (100%)
VISG (Reach-to-grasp task)				
Visuomotor Object	7 (22%)	9 (28%)	16 (50%)	32 (100%)
Visual Object	2 (11%)	3 (17%)	13 (72%)	18 (100%)

Figure captions

Figure 1

Tested objects and tasks. A) Representation of the 5 objects tested and of the grip types used by the monkey: from left to right, ball (grasped with the whole hand), handle (grasped with finger prehension), ring (grasped with the index finger), plate (grasped with a primitive precision grip), cylinder-in-groove (grasped with an advanced precision grip). B) Time course and time epochs in the Reach-to-Grasp task in the light and in the dark. The sequence of status of the Home Button, color of the fixation point (Fixation LED), status of the light illuminating the object (Illumination) in dark and in light condition, and status of the Target object are shown. Below the diagram, typical examples of eye traces during a single trial and time epochs are shown. Dashed lines indicate task and behavioral markers: trial start (Home Button push), fixation target appearance (Fixation LED green), eye traces entering the fixation window, object illumination onset (illumination on, both for light and dark conditions), object illumination offset (illumination off, only in dark condition), go signal for reach-to-grasp movement (Fixation LED red), movement onset (Home Button release), movement offset (Target object holding), fixation target switching off (Fixation LED off), Target object release (off, coincident with object illumination off in light condition). Rectangles below time course indicate functional time epochs. Above the time course, cartoons of the trial sequence are shown. C) Time course and time epochs in the Observation task. The sequence of status of Home Button, Fixation LED, Illumination of the object (illumination), and eye traces are shown. Markers are, from left to right: trial start (Home Button push), fixation target appearance (Fixation LED green), eye traces entering the fixation window, object illumination on (Illumination on), go signal for home button release (Fixation LED red), Home Button release, coincident with illumination off. All other details as in B).

Figure 2

Population data. A) Distribution of the incidence of significant effects modulating V6A cells during the time-course of the task. Histograms show the results of two-way ANOVA as incidence of modulated cells during the grasping preparation (epoch DELAY), execution (epoch MOV) and object holding (epoch HOLD). The results are shown with respect to effect complexity, that is, from left to right, the main effects and the effect of both factors. Numbers of modulated cells: effect of visual condition: N= 57 (DELAY), N= 36 (MOV), N= 39 (HOLD); effect of grip type: N= 34 (DELAY), N= 52 (MOV), N= 42 (HOLD); effect of both visual condition and grip type: N= 113 (DELAY), N= 163 (MOV), N= 165 (HOLD); no effect (not shown in the figure): N= 71 (DELAY), N= 25 (MOV), N= 30 (HOLD). B) Percentage of tuned cells by grip type (continuous line) and visual condition (dashed line) in a sliding window ANOVA (width: 200 ms, centered on each data point). Trials are aligned on the 2 arrowheads: illumination of the object (light onset) and movement onset. Rectangles below each plot indicate the functional time epochs (VISG, DELAY, MOV, HOLD).

Figure 3

Example of the discharge of a V6A *Visual* neuron (A) and of a *Motor* neuron (B) to five different grips and to two visual backgrounds. A) Top: type of handgrips. Middle: peristimulus time histograms. Horizontal scale: 200 ms/div. Vertical scale bar on histogram: 37 spikes/s; eye traces: 60°/division. Rectangles below histograms indicate the duration of the epochs FREE (Fr), FIX (F), VISG (V), DELAY (D), MOV (M), HOLD (H). Data collected in the dark are depicted in black, those collected in the light are in red. Below histogram: raster displays of impulse activity. Behavioral markers are depicted in different colors: green: fixation point onset; yellow: illumination onset; black: illumination offset, in the dark condition; red: go signal; blue: movement onset: brown: movement end. Bottom: record of horizontal (upper trace) and vertical components (lower trace) of eye movements, shown with the same alignment as the neural activity. The activity of cells in each plot was aligned twice, on fixation onset and on arm movement onset (two continuous

vertical lines), with a dashed vertical line indicating the interruption of the trials to obtain the double alignment. (B) All conventions are as in A, vertical scale on histogram: 77 spikes/s.

Figure 4

Neuronal examples of *Visuomotor* neurons. A-B) Example of a V6A *Visuomotor Object-type* neuron. Neural discharge in the Reach-to-Grasp task (A) and in the Observation task (B). Vertical scale bar on histogram: 60 spikes/s. C-D) Example of a V6A *Visuomotor Nonobject-type* neuron. Discharge in the Reach-to-Grasp task (C) and in the Observation task (D). Vertical scale bar on histogram: 118 spikes/s. In the Observation task, rectangles below histograms indicate the duration of the epochs VIS (V) and LONGVIS (LV) that capture the transient and the sustained visual response to object presentation. Rasters, histograms and recordings of x and y components of eye position are aligned (vertical bar) on the onset of the Reach-to-Grasp movement (A, C) and on the object illumination (A, B, C, D). Other conventions as in Fig. 3.

Figure 5

Population activity of different categories of V6A cells. Visuomotor (A, N= 92, 39%) and Visual (B, N= 74, 31%), population discharges, divided into Object and Nonobject-type, and Motor (C, N= 72, 30%), expressed as averaged spike density functions (SDFs), where red lines indicate neural activity recorded in the light; black lines indicate activity in the dark. The thin lines indicate the variability band (SEM). Lines above epoch rectangles indicate epochs where the permutation test ($p<0.05$) was significant. All other conventions are as in Fig. 3.

Figure 6

Results from demixed principal components (dPCA). A) Cumulative signal variance explained by PCA (black) and dPCA (grey). Demixed PCA explains almost the same amount of variance as

standard PCA. B) Variance of the individual demixed principal components. Each bar shows the proportion of total variance. Pie chart shows how the total signal variance is split between parameters (visual condition, and grip). C, D, E) Time course of the signal of single components: C) Condition-independent; D) Grip type; E) Visual condition. For the grip component, the separation of the different grips starts well before the grasp onset (arrow) and continues till grasp completion.

Figure 7

Comparison of cell categories between V6A and AIP. A) Incidence of different categories of cells. Distribution of Visual (Object-type, Nonobject-type), Visuomotor (Object-type, Nonobject-type) and Motor cells in V6A (black bars) and in AIP (white hatched bars) (Chi-Squared test: n.s.). Data of area AIP were derived by averaging the data reported in studies of AIP from Sakata's lab (Sakata et al., 1995; Murata et al., 1996, 2000). B-C) Distribution of different categories of cells on the basis of their selectivity in V6A (B) and AIP (C) (Chi-Squared test: n.s.). Data of area AIP were taken from Murata et al., (2000).

Figure 8

Comparison between grasp-related properties of V6A and AIP. A) Percentage of tuned cells in a sliding window one-way ANOVA in time steps of 1ms in V6A (thick black; N=276) and AIP (thin black). The plot of AIP was redrawn from fig. 3B of Schaffelhofer and Scherberger (2016). Plots are aligned on object illumination onset and on movement onset (vertical lines). B) Preferred grip types in V6A (top) and AIP (bottom). Pie charts show the distribution of preferred grip type in various task epochs. The percentage of cells preferring precision grip is represented in white, the power grip in black/hatched black. C) Grip type tuning consistency across task epochs in V6A (left) and AIP (right), data from fig. 7A in Baumann et al. (2009). Histogram bars indicate the percentage of cells that stay tuned for the same grip (black-hatched black), change preference to the opposite grip (grey-hatched gray) or lose their tuning (white) when transitioning between consecutive task

epochs (Visg/Delay and Delay/Mov). Significance level was chosen as 0.01, as performed by Baumann et al. (2009). AIP data were taken from fig. 8 of Baumann et al. (2009). The terms CUE-PLAN-MOVE used for AIP are those of Baumann et al. (2009), but are qualitatively similar to VISG-DELAY-MOV used for V6A.

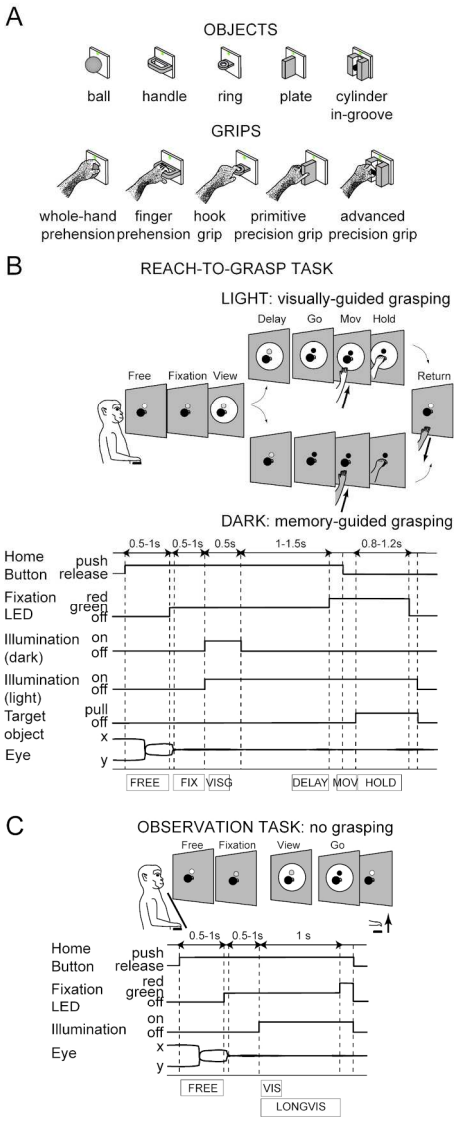

Figure 1
Breveglieri et al.

Figure 1
Tested objects and tasks. A) Representation of the 5 objects tested and of the grip types used by the monkey: from left to right, ball (grasped with the whole hand), handle (grasped with finger prehension), ring (grasped with the index finger), plate (grasped with a primitive precision grip), cylinder-in-groove (grasped with an advanced precision grip). B) Time course and time epochs in the Reach-to-Grasp task in the light and in the dark. The sequence of status of the Home Button, color of the fixation point (Fixation LED), status of the light illuminating the object (Illumination) in dark and in light condition, and status of the Target object are shown. Below the diagram, typical examples of eye traces during a single trial and time epochs are shown. Dashed lines indicate task and behavioral markers: trial start (Home Button push), fixation target appearance (Fixation LED green), eye traces entering the fixation window, object illumination onset (illumination on, both for light and dark conditions), object illumination offset (illumination off, only in dark condition), go signal for reach-to-grasp movement (Fixation LED red), movement onset (Home Button release), movement offset (Target object holding), fixation target switching off (Fixation LED off), Target

object release (off, coincident with object illumination off in light condition). Rectangles below time course indicate functional time epochs. Above the time course, cartoons of the trial sequence are shown. C) Time course and time epochs in the Observation task. The sequence of status of Home Button, Fixation LED, Illumination of the object (illumination), and eye traces are shown. Markers are, from left to right: trial start (Home Button push), fixation target appearance (Fixation LED green), eye traces entering the fixation window, object illumination on (Illumination on), go signal for home button release (Fixation LED red), Home Button release, coincident with illumination off. All other details as in B).

84x226mm (300 x 300 DPI)

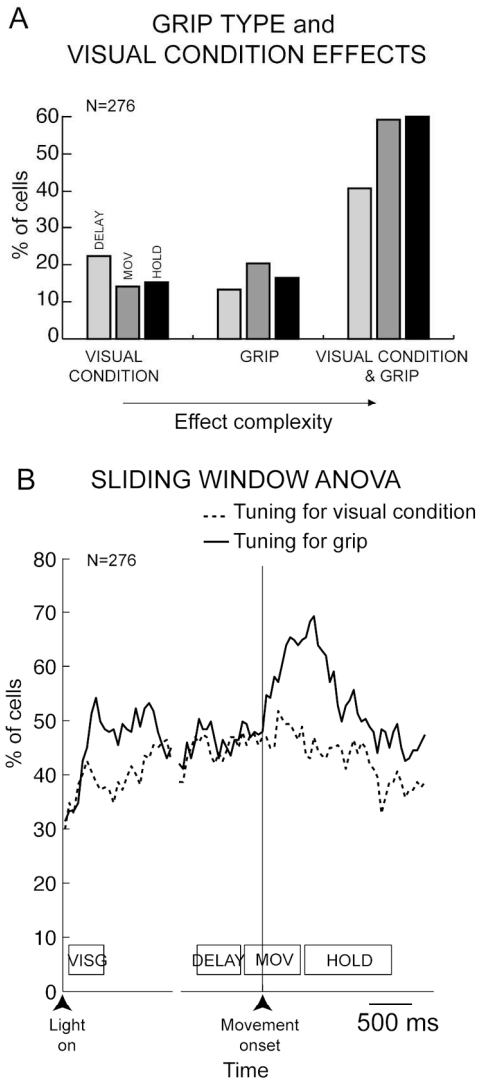

Figure 2
Breveglieri et al.

Figure 2
Population data. A) Distribution of the incidence of significant effects modulating V6A cells during the time-course of the task. Histograms show the results of two-way ANOVA as incidence of modulated cells during the grasping preparation (epoch DELAY), execution (epoch MOV) and object holding (epoch HOLD). The results are shown with respect to effect complexity, that is, from left to right, the main effects and the effect of both factors. Numbers of modulated cells: effect of visual condition: N= 57 (DELAY), N= 36 (MOV), N= 39 (HOLD); effect of grip type: N= 34 (DELAY), N= 52 (MOV), N= 42 (HOLD); effect of both visual condition and grip type: N= 113 (DELAY), N= 163 (MOV), N= 165 (HOLD); no effect (not shown in the figure): N= 71 (DELAY), N= 25 (MOV), N= 30 (HOLD). B) Percentage of tuned cells by grip type (continuous line) and visual condition (dashed line) in a sliding window ANOVA (width: 200 ms, centered on each data point). Trials are aligned on the 2 arrowheads: illumination of the object (light onset) and movement onset. Rectangles below each plot indicate the functional time epochs (VISG, DELAY, MOV, HOLD).

79x201mm (300 x 300 DPI)

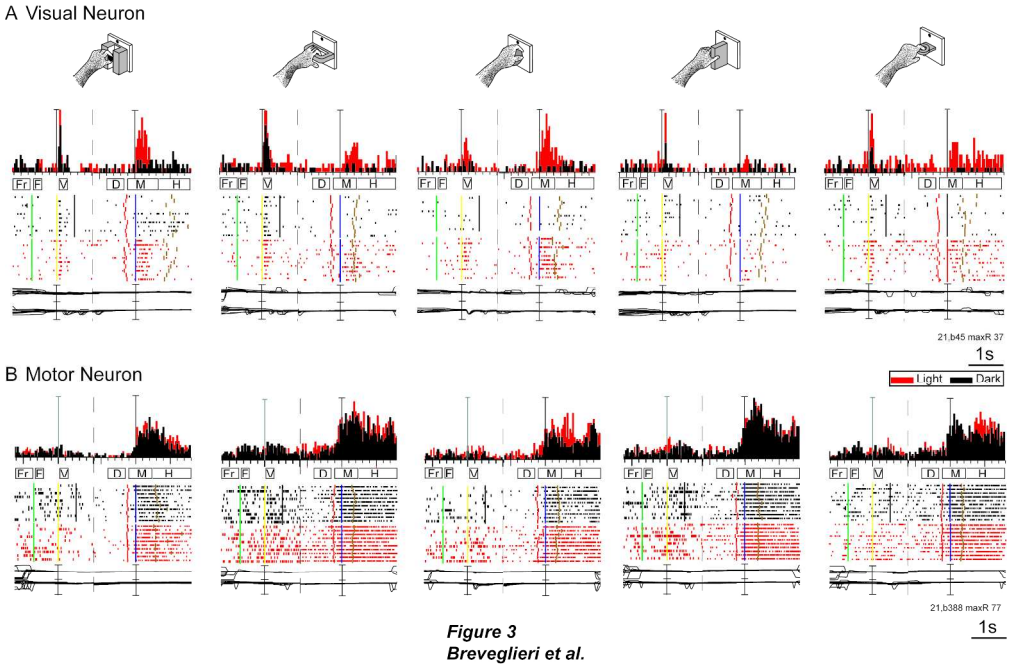

Figure 3
Example of the discharge of a V6A Visual neuron (A) and of a Motor neuron (B) to five different grips and to two visual backgrounds. A) Top: type of handgrips. Middle: peristimulus time histograms. Horizontal scale: 200 ms/div. Vertical scale bar on histogram: 37 spikes/s; eye traces: 60°/division.¬ Rectangles below histograms indicate the duration of the epochs FREE (Fr), FIX (F), VISG (V), DELAY (D), MOV (M), HOLD (H). Data collected in the dark are depicted in black, those collected in the light are in red. Below histogram: raster displays of impulse activity. Behavioral markers are depicted in different colors: green: fixation point onset; yellow: illumination onset; black: illumination offset, in the dark condition; red: go signal; blue: movement onset: brown: movement end. Bottom: record of horizontal (upper trace) and vertical components (lower trace) of eye movements, shown with the same alignment as the neural activity. The activity of cells in each plot was aligned twice, on fixation onset and on arm movement onset (two continuous vertical lines), with a dashed vertical line indicating the interruption of the trials to obtain the double alignment. (B) All conventions are as in A, vertical scale on histogram: 77 spikes/s.

235x156mm (300 x 300 DPI)

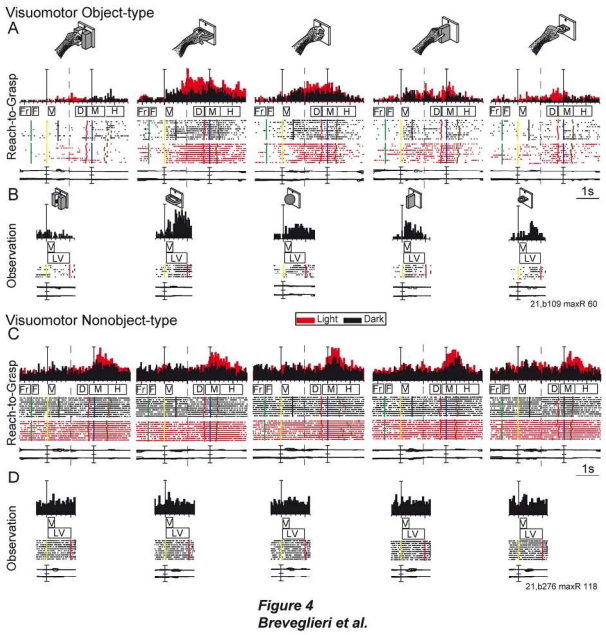

Figure 4
Neuronal examples of Visuomotor neurons. A-B) Example of a V6A Visuomotor Object-type neuron. Neural discharge in the Reach-to-Grasp task (A) and in the Observation task (B). Vertical scale bar on histogram: 60 spikes/s. C-D) Example of a V6A Visuomotor Nonobject-type neuron. Discharge in the Reach-to-Grasp task (C) and in the Observation task (D). Vertical scale bar on histogram: 118 spikes/s. In the Observation task, rectangles below histograms indicate the duration of the epochs VIS (V) and LONGVIS (LV) that capture the transient and the sustained visual response to object presentation. Rasters, histograms and recordings of x and y components of eye position are aligned (vertical bar) on the onset of the Reach-to-Grasp movement (A, C) and on the object illumination (A, B, C, D). Other conventions as in Fig. 3.

209x148mm (300 x 300 DPI)

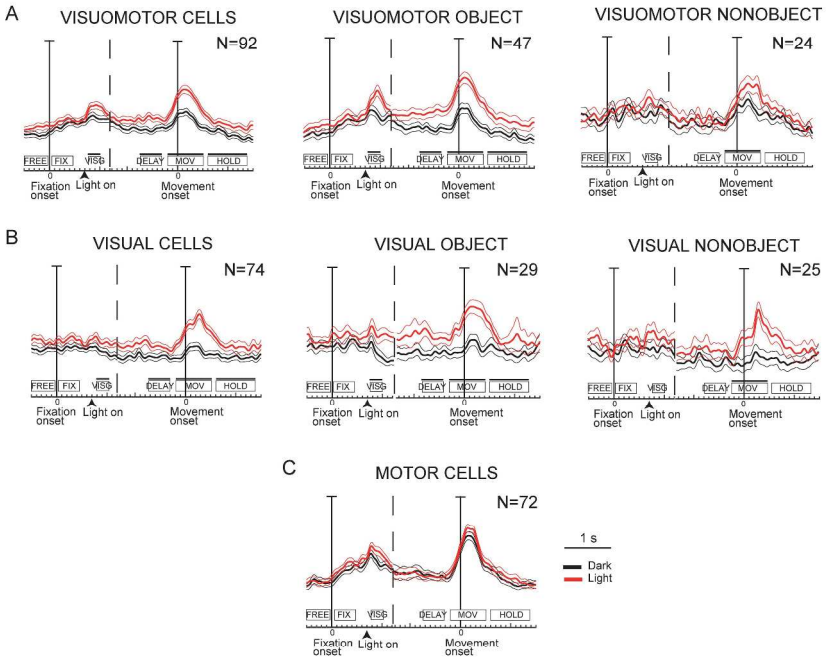

Figure 5
Breveglieri et al.

Figure 5
Population activity of different categories of V6A cells. Visuomotor (A, N= 92, 39%) and Visual (B, N= 74, 31%), population discharges, divided into Object and Nonobject-type, and Motor (C, N= 72, 30%), expressed as averaged spike density functions (SDFs), where red lines indicate neural activity recorded in the light; black lines indicate activity in the dark. The thin lines indicate the variability band (SEM). Lines above epoch rectangles indicate epochs where the permutation test ($p<0.05$) was significant. All other conventions are as in Fig. 3.

297x420mm (300 x 300 DPI)

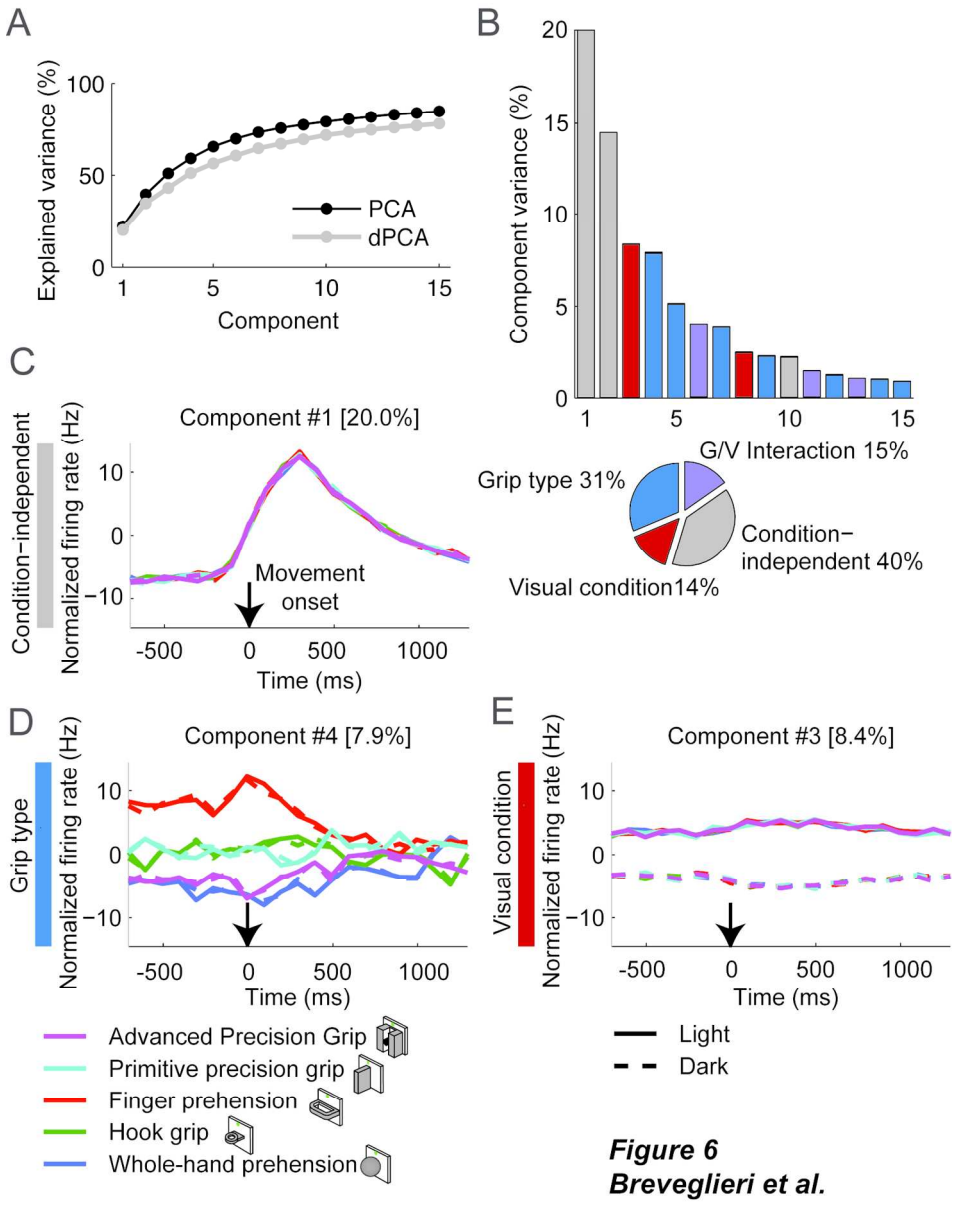

Figure 6
Results from demixed principal components (dPCA). A) Cumulative signal variance explained by PCA (black) and dPCA (grey). Demixed PCA explains almost the same amount of variance as standard PCA. B) Variance of the individual demixed principal components. Each bar shows the proportion of total variance. Pie chart shows how the total signal variance is split between parameters (visual condition, and grip). C, D, E) Time course of the signal of single components: C) Condition-independent; D) Grip type; E) Visual condition. For the grip component, the separation of the different grips starts well before the grasp onset (arrow) and continues till grasp completion.

142x180mm (300 x 300 DPI)

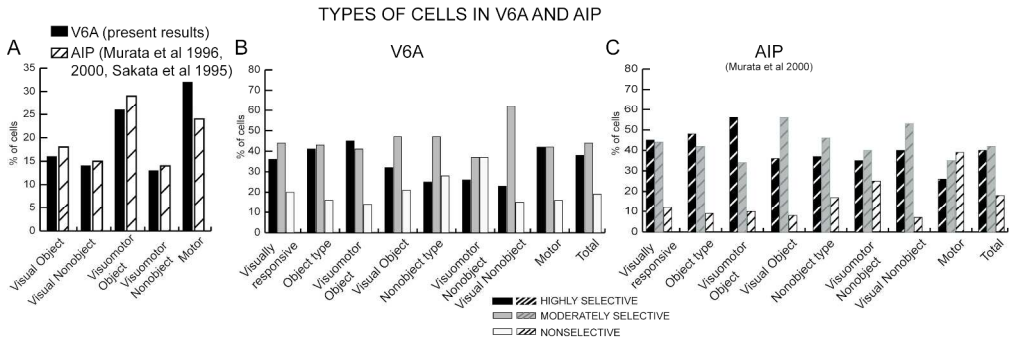

Figure 7
Breveglieri et al.

Figure 7
Comparison of cell categories between V6A and AIP. A) Incidence of different categories of cells. Distribution of Visual (Object-type, Nonobject-type), Visuomotor (Object-type, Nonobject-type) and Motor cells in V6A (black bars) and in AIP (white hatched bars) (Chi-Squared test: n.s.). Data of area AIP were derived by averaging the data reported in studies of AIP from Sakata's lab (Sakata et al., 1995; Murata et al., 1996, 2000). B-C) Distribution of different categories of cells on the basis of their selectivity in V6A (B) and AIP (C) (Chi-Squared test: n.s.). Data of area AIP were taken from Murata et al., (2000).

238x96mm (300 x 300 DPI)

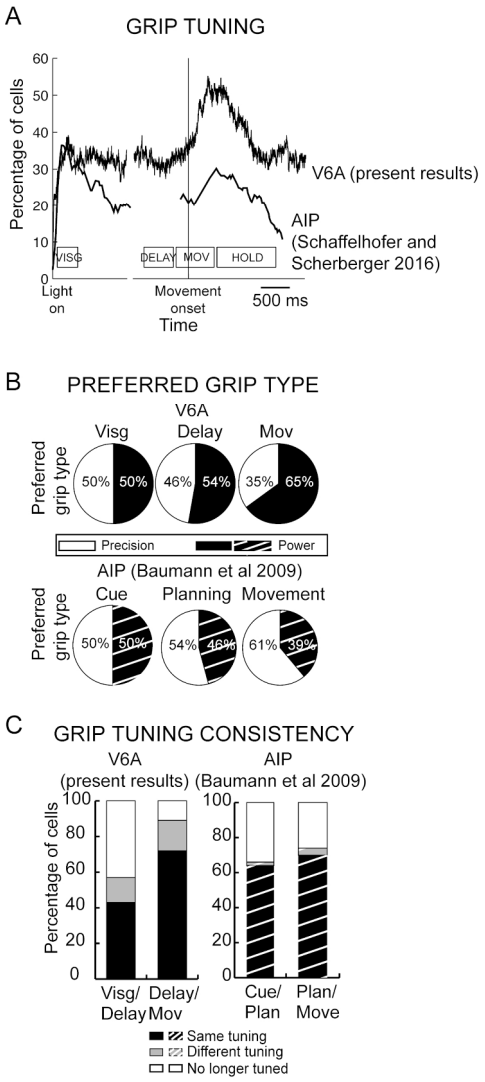

Figure 8
Breveglieri et al.

Figure 8
Comparison between grasp-related properties of V6A and AIP. A) Percentage of tuned cells in a sliding window one-way ANOVA in time steps of 1ms in V6A (thick black; N=276) and AIP (thin black). The plot of AIP was redrawn from fig. 3B of Schaffelhofer and Scherberger (2016). Plots are aligned on object illumination onset and on movement onset (vertical lines). B) Preferred grip types in V6A (top) and AIP (bottom). Pie charts show the distribution of preferred grip type in various task epochs. The percentage of cells preferring precision grip is represented in white, the power grip in black/hatched black. C) Grip type tuning consistency across task epochs in V6A (left) and AIP (right), data from fig. 7A in Baumann et al. (2009). Histogram bars indicate the percentage of cells that stay tuned for the same grip (black-hatched black), change preference to the opposite grip (grey-hatched gray) or lose their tuning (white) when transitioning between consecutive task epochs (Visg/Delay and Delay/Mov). Significance level was chosen as 0.01, as performed by Baumann et al. (2009). AIP data were taken from fig. 8 of Baumann et al. (2009). The terms CUE-PLAN-MOVE used for AIP are those of Baumann et al. (2009), but are qualitatively similar to

VISG-DELAY-MOV used for V6A.

93x237mm (300 x 300 DPI)